

Biology and Behavior of *Damon variegatus* Perty of South Africa  
and *Admetus barbadensis* Pocock of Trinidad, W.I.  
(Arachnida, Pedipalpi)<sup>1</sup>

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(Text-figures 1-5)

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INTRODUCTION

**T**AILLESS whip-scorpions or scorpion-spiders are dorsally flattened, cryptically colored arachnids, found in tropical and sub-tropical regions. Their systematic position is controversial so that a study of their biology and behavior is not only interesting in its own right, but might also be relevant to this question. The scorpion-spiders have traditionally been placed in the arachnid order Pedipalpi, but in 1949 Millot replaced this by two new orders, the Uropygi and the Amblypygi, the latter containing the scorpion-spiders. Subsequently Petrunkevitch (1955) has divided the Pedipalpi into three separate orders, the Thelyphonida (true whip-scorpions), the Schizomida and the Phrynichida

(scorpion-spiders). He agrees with Millot, however, that the first two are more closely related to each other than either are to the scorpion-spiders. Both of these proposals imply that the previous order Pedipalpi reflected similarities which had in fact arisen in two separate lines of evolution. All these conclusions have been reached from a consideration of the morphology of the animals, the more recent suggestions taking into account the internal as well as external features. It seemed possible that behavioral characteristics might supply evidence for or against the suggested convergence of the Schizomida and Thelyphonida with the Phrynichida. Few records have been made of the behavior of the Pedipalpi as a whole and this dearth of information is especially noticeable in the case of the Phrynichida. The present observations on *Admetus barbadensis* and *Damon variegatus*, both members of the family Tarantulidae, are offered in view of this lack. It is hoped that if they serve no other purpose, they may provide some incentive to record the equivalent information for the other two groups; for until comparative studies have been made on the animals as a whole, much of what is said here must remain a speculative contribution to the subject of pedipalp relationships.

HABITAT

In the field these scorpion-spiders can be found beneath loose pieces of wood or leaves, more especially under forest cover. There is no indication that they ever construct burrows for themselves either in the wild or in the laboratory, as has also been reported by Gravelly (1915) for the East Indian scorpion-spiders. If the cover is suddenly removed from a specimen, it may stay absolutely still, presumably employing behavior

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<sup>2</sup>Some of the observations recorded here were made in Trinidad on a visit to the field station of the Department of Tropical Research and thanks are due both the staff of the station and the Society for making this visit possible. Financial assistance is also gratefully acknowledged from the National Science Foundation, the South African Council for Scientific and Industrial Research and the Royal Commission for the Exhibition of 1851.

which would sometimes lead to its being overlooked because of its general flatness and cryptic coloration. If it moves, it does so quickly, running suddenly sideways onto another surface of the covering object or away to another hiding place. It never threatens unless it has actually been picked up and then only occasionally.

*D. variegatus* is more markedly synanthropic than *A. barbadensis* and in many parts of Natal can be collected very readily from cellars, out-houses or man-holes where it lives either in crevices or freely on the walls if the place is fairly dark. This acceptance of human habitation is a biological feature which contrasts with the behavior of the schizomids and thelyphonids, neither of which has been reported to occur associated with man.

In laboratory conditions both *A. barbadensis* and *D. variegatus* show a diurnal rhythm of activity in which the active phase is nocturnal and since the former species has been found wandering about at night in the forests of Trinidad, it is assumed that the activity pattern shown in the laboratory is a natural one and not induced by disturbances during the day. Similar habits occur in the other two groups but it is common for most arachnids to be nocturnal.

#### FEEDING

There is no information about what the scorpion-spiders eat in the field. Prey is, however, caught at night and is almost certainly living. Animals such as moths, crickets, spiders, cockroaches and beetles are cricked in the laboratory and probably form part of the normal diet. In stalking prey, the scorpion-spider approaches directly, *i.e.*, not sideways as in escape. The tips of the first pair of legs<sup>8</sup> tap the prey so gently that they seldom disturb it. When the scorpion-spider is an inch or two from its prey, it suddenly throws itself upon the insect, clutching at it with the exposed spines of both pedipalps. Sometimes, when the prey is especially large, the scorpion-spider attacks several times in this manner, retreating between each attack. More usually the insect is impaled on the pedipalpal spines at the first onslaught. Once the prey is caught, the pedipalps fold, pulling it towards the mouth and retaining their hold of it while the needle-like chelicerae alternately dig down into it.

After the meal the corpse is often left as a mangled mass of exoskeleton but this is not invariably so; sometimes it remains almost entire,

only showing external damage at the points where the chelicerae had punctured it. This is strongly reminiscent of what occurs among the spiders and suggests that scorpion-spiders may also rely on extra-oral digestion to a considerable extent.

Such a consideration leads directly to the problem of how the food is conveyed into the gut, once it has been liquified by the digestive juices. Just behind the mouth opening there is a typically arachnid sucking pharynx and ingestion itself consists of drawing up the fluid contents of the corpse into this sac.

Both scorpions and scorpion-spiders possess "pseudotracheal" areas on certain limbs. In the scorpions such filter-like areas are located on the coxal endites of the second legs. During feeding either digestive juices pass through these and onto the food or the liquified food passes through them into the gut: there is no decisive evidence as yet to distinguish between these possibilities. Limb movements, which occur during feeding, could help move the fluid in either direction. In the scorpion-spiders there is no limb movement, yet on each coxa of the pedipalps they have a pseudotracheal area structurally resembling the pseudotracheae of a scorpion. The main channel, like that in the scorpions, opens into the base of the esophagus.

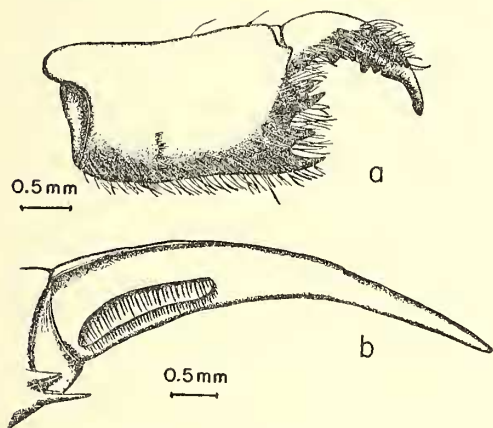
In captivity scorpion-spiders frequently drink water. In this behavior, as in the eating pattern, there are alternate movements of the chelicerae. These cease for short intervals as fluid is drawn up into the gut. The significance of the cheliceral movements is obscure; perhaps they are merely a reflection of the fact that the animal uses the motor pattern of normal feeding when drinking free water. Conversely, the similarity of the eating and drinking patterns is in keeping with the suggestion that it is a fluid which is taken up into the mouth during feeding and that extra-oral digestion must occur.

As with the detection of prey, the detection of water appears to be done by sense organs on the feelers. This may be demonstrated as follows: A desiccated animal is put on the bottom of a dish which has a number of small holes bored in its lid and many drops of water placed between these holes. During its investigation of the dish, the scorpion-spider will eventually put one of its feelers up through a hole and into a drop of water. Immediately, the behavior pattern of drinking can be seen in the animal below and it will make efforts to get at the water. The sense organs involved have not yet been identified, nor is it clear whether the feelers only can be used for detecting water.

<sup>8</sup> The first legs are very long and antenniform and will be referred to throughout this study as the "feelers;" see Patten (1917).

## WASHING

This behavior may be seen most frequently after the animals have been drinking or eating, though they will interrupt other behavior, such as courting or fighting, to wash themselves. The feelers and walking legs are pulled to the mouth by the pedipalps and then drawn between the chelicerae, being cleaned by the medial brushes which occur on these appendages (Text-fig. 1a). During washing, the chelicerae move up and down as they do in eating or drinking.



TEXT-FIG. 1. a—Lateral view of the left chelicera of *A. barbadensis*, showing the mesial brushes on both first and second segments. b—Lateral view of the last segment of the pedipalp of *A. barbadensis*, showing the structure used by the animal for washing its limbs.

The catching of a leg or feeler by the pedipalp may occur as a preliminary to its being washed between the chelicerae, as described above, but the action may also be repeated over and over again without the chelicerae being involved at all; the limb is pulled a short distance towards the mouth by the pedipalp and then released. Here the pedipalp itself is doing the cleaning: the apparatus concerned is a little close-haired brush on the last segment (Text-fig. 1b)<sup>4</sup>. The limb is drawn through this brush as it returns to its position after being pulled towards the mouth. The important function of the cleaning brush, however, is the washing of the pedipalps themselves. Though the brushes of the chelicerae are able to clean some of the spines on the inner surface of the pedipalp, this cleaning action is incomplete and many of the pedipalpal spines

are not reached at all. If the pedipalpal spines are to act as weapons, their sharpness is all-important. This must depend on their being kept free of congealed remnants of prey and dirt and it is desirable that there should be a mechanism for cleaning them properly. It is the pedipalpal brushes which do the major part of this cleaning, wiping each of the large spines in turn, then cleaning the outer surface of the pedipalp itself. The brushes are themselves cleaned on the cheliceral hairs, these being moistened at the mouth. It seems possible that the brush on the pedipalp of *D. variegatus* and *A. barbadensis* has been evolved primarily for the cleaning of these pedipalpal spines. Millot (1949) shows the presence of the brush in his illustration of *Charinus milloti* Fage, a member of the Charontidae, the second family of Phrynichida. So pedipalpal brushes may occur throughout the whole order; possibly they were one of the prerequisites for the capitalization of the pedipalpal spines as weapons.

## INTRASPECIFIC BEHAVIOR

Aggressive and threatening behavior occurs in encounters between two males or two females, between an adult and a young animal or even between two young animals, and the same behavior comprises the first part of courtship in any pair of scorpion-spiders. Hence a description of actual courtship behavior will be left until after consideration of intraspecific behavior which does not lead up to mating.

In an encounter between individuals that are clearly unevenly matched, (*i.e.*, a small and a large individual or one injured and one intact), regardless of which touches the other first, the result is almost always the same. The "inferior" animal runs off sideways for a short distance and then extends the nearer feeler towards the superior animal, quivering it violently in the air over the body of the other. Then, without necessarily any further move from its antagonist, the weaker will suddenly fold in its feelers and run off as far as possible from the other. Sometimes the superior animal may unfold its pedipalps and threaten or even rush and fling itself at the inferior. Invariably, however, the latter animal escapes uninjured from the first encounter. In laboratory observations it may subsequently be killed, but such an event should perhaps be regarded as something that would not normally occur in the field; it seems to happen only when the weaker animal is allowed no space for escape.

When the contestants are more evenly matched, the first encounter may, as in the previous case, include violent pedipalpal attack. Here the two animals will strike at each other

<sup>4</sup> It is this structure that Barnard, *Ann. Mag. nat. hist.* (6), 11, 28-30 (1893), suggested was a sense organ, and the homologue of the adhesive organ on the last segment of the pedipalp of the solifugid.

with one or both pedipalps. The spines on these appendages may tear the carapace or abdominal tergites or rip open the swollen intersegmental membranes of the pedipalps where they are exposed in threatening. Such wounds are often fatal and, if the stricken animal is not eaten immediately by its opponent, it will usually be dead by the following day.

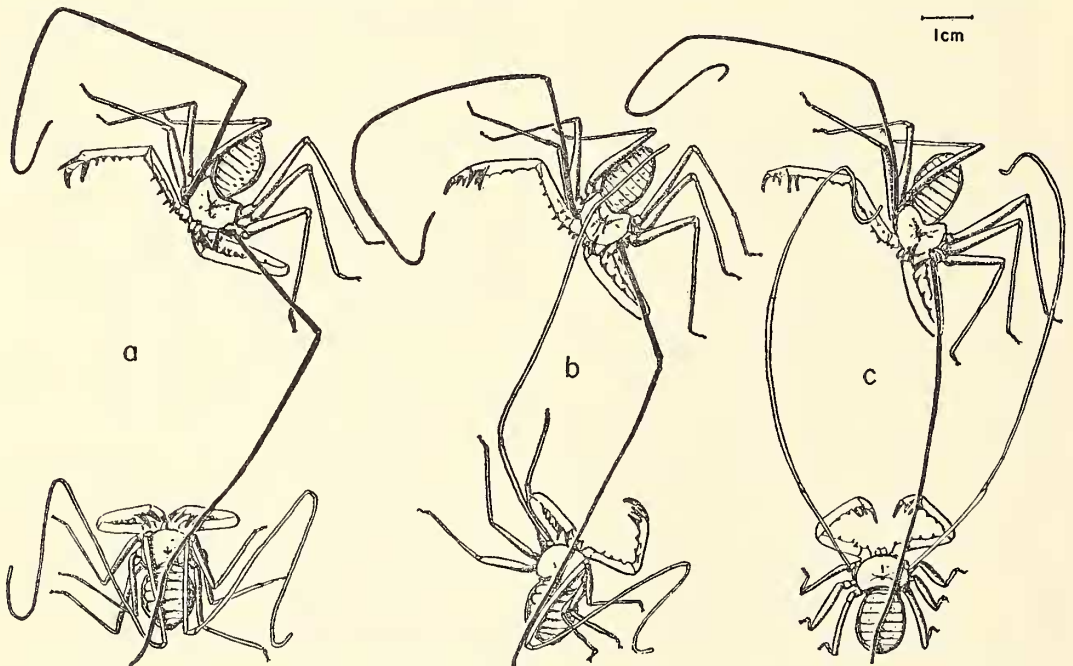
In addition to these direct attacks, however, there are numerous conflicts that end without any blood being shed. Such encounters may be described as threat fights and they precede almost all true courtship. There are several variations, but in general the victor must beat its opponent into submission using only its delicate feelers. Although the blows may be given with such force that the body of the opponent sways beneath them, it is obvious that little discomfort, let alone hurt, could come from them. This would appear to be a case of highly ritualized threatening which does not involve the weapons of offence themselves.

The commonest form of threatening is what is here called "side-tapping." The animal con-

cerned faces about 45° away from its opponent, (Text-fig. 2a), bends its abdomen so that it is more nearly in line with the opponent, extends and opens the pedipalp furthest from the enemy and taps or beats the latter's body with the nearer feeler, which is stretched out in front. The body of the animal doing the tapping is nearly always held very close to the ground, as if it needs support.

The opponent normally does one of two things: either it returns the tapping, using precisely the same pose as does the first animal so that a very symmetrical effect is achieved (Text fig. 2b) or it stands up, holds its body well away from the ground and allows the first to beat at it (Text-fig. 2c). If the latter response is made, the animal which is being beaten usually extends its pedipalps to some extent, drawing the tips fairly close together and keeping the claws (formed by the spines) closed, *i.e.*, not using the normal threat pose in which the pedipalps are both extended and opened.

Whether there is mutual side-tapping or whether only one animal taps, the behavior lasts



TEXT-FIG. 2. Diagrammatic representation of an encounter between two specimens of *D. variegatus*. Animal I is above, with its feelers represented in black, Animal II is below and is the smaller. In all cases the full length of the feeler of Animal I is not shown in proportion to its body. **a**—Animal I is side-tapping, leading with the left feeler while the right is folded back. **b**—Animal I is side-tapping slightly more actively, as can be seen from the fact that its body is more fully oriented towards II and it has opened and extended its right pedipalp further. Animal II is now returning the side-tapping so that there is a mutual exchange of blows. **c**—Animal I has gone into what is virtually the extreme side-tapping pose while II has taken up the "passive" stance, with legs raising the body high above the substratum while the pedipalps are half extended and the claws almost completely closed. The feelers curve forward gently and touch at II.

only a short time and then there is a reorganization. In the case of mutual side-tapping, the pair pull in their feelers and face each other. Then they gradually revert to side-tapping once more but this time leading with the other feeler. Before the new orientation and as the animals face each other, the feelers may exchange a few beats. Occasionally, after coming forward to change, the pair revert to leading with the same feeler as they were using before. Less frequently, one animal will change its leading feeler while the other will not, thus producing a thoroughly disorganized side-tapping.

If only one animal of the pair has been tapping, and the other is passive, the roles are reversed periodically; thus the passive scorpion-spider begins to tap while its partner rises up on its legs, brings both pedipalps to the half-extended position and holds its feelers partly back, *i.e.*, it assumes the passive role.

Another behavior pattern can be distinguished; this seems to occur in animals which are both more active than the couples described above. Each stands with its pedipalps open and partly, or even widely extended and then the animals lunge in turn towards each other. Sometimes they spike the body or one of the limbs but quite frequently they miss altogether. Sometimes both animals strike together and the spines of the two pairs of pedipalps become entangled. A slight variation of this pattern is one in which both animals move sideways, facing each other and occasionally lunging across the space that separates them. In some cases the same dance-like steps occur but the animals merely beat at each other with their feelers instead of using their more offensive pedipalps.

These various patterns may merge into one another or change abruptly from one to the other; there is as yet no clear explanation of the significance of each, or of why or how the changes are initiated. The sequence does not seem to have any precise bearing on the final result of the encounter. This latter takes one of three forms. Firstly, there may be a serious pedipalpal exchange between the pair and in this one or both may be injured or killed. Secondly, one of the pair may suddenly turn and run off rapidly (behavior that does not normally follow a series of active tapping at the opponent). Lastly, one or both of the animals may just wander off slowly and pay no further attention to the other.

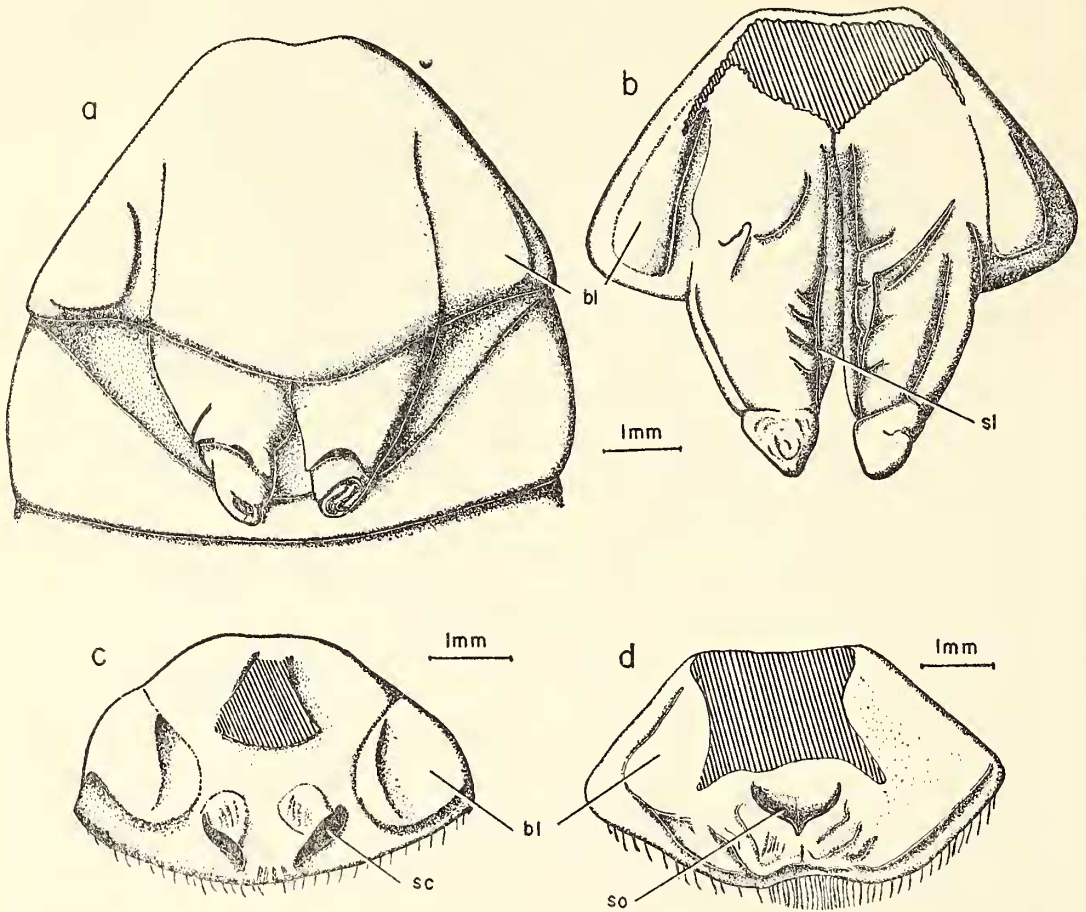
#### COURTSHIP

True courtship is far more difficult to observe than the encounters recorded so far. The chances of seeing this behavior, however, are increased if the observations are made at night and under

a very dim or red light. In neither *D. variegatus* nor *A. barbadensis* can the sexes be distinguished from a glance at the dorsal surface and so, for experimental work, it is convenient to determine the sex of each animal and mark its back with appropriate paint. Sexing can be done using the differences in the details of the furrows on the genital operculum, as was suggested for *D. variegatus* by Lawrence (1949). With live animals, however, it is better to hold the animal on its back and lift the edge of its operculum gently; if it is a male, the genital organs will be extruded (Text-fig. 3a). These male organs will be referred to here as "genital cones." (The term "penes" used by Lawrence (1949) is unacceptable for, as will be seen later, they do not function as intromittent organs). They are relatively larger in *A. barbadensis* than in *D. variegatus* and consist of a pair of conical structures (Text-fig. 3b) almost joined together at their bases, each opening towards the midline by way of many peculiar foldings. The male ducts lead into the bases of these genital cones.

The under surface of the female operculum bears no such organs, but in the female *A. barbadensis* there is a pair of small dark-colored sclerites lying obliquely just under the operculum (Text-fig. 3c). These point towards the midline and are attached anteriorly. Their function will be discussed later in relation to the egg-case. The female *D. variegatus* lacks these sclerites and has instead a number of complicated foldings of the cuticle, some of which are sclerotized (Text-fig. 3d). In either case the single opening of the female duct lies at the base of the operculum.

Returning to the actual courtship, it has already been said that this is normally preceded by certain behavior patterns which also occur in encounters between animals of the same sex or immature stages. In the first part of an encounter the degree of violence may vary widely, but eventually, if genuine courtship is to follow, the animals will reach a stage when the female response to the side-tapping of the male becomes one of submission. Instead of holding her body stiffly away from the ground, she allows it to come to rest, spreading her legs out sideways. Her pedipalps are folded from the semi-extended position into one of rest and her feelers become motionless. The male then straightens his body and comes forward to face her; he beats her intermittently with both feelers. Presently he extends his pedipalps fairly slowly and lunges at her, pushing her with his body as if testing her passivity. During these advances, the female may show signs of recurring aggression and immediately the male will move back and again



TEXT-FIG. 3. **a**—Genital area of *A. barbadensis* showing the extruded genital cones. **b**—View of the genital cones from the undersurface of the genital operculum. The male ducts and accessory glands would empty into the cones through that part which is shown by cross-hatching in the diagram. Part of the slit-like opening of the cones can be seen, **sl**. **c**—Undersurface of the genital operculum of a female *A. barbadensis* to show the sclerites, **sc**, which hold the anterior end of the egg-case. **d**—Undersurface of the genital operculum of a female *D. variegatus* showing the foldings and sclerotization which occur there in the formation of a socket, **so**, into which the anterior end of the egg-case is moulded. The position of the first pair of book-lungs can be seen, **bl**.

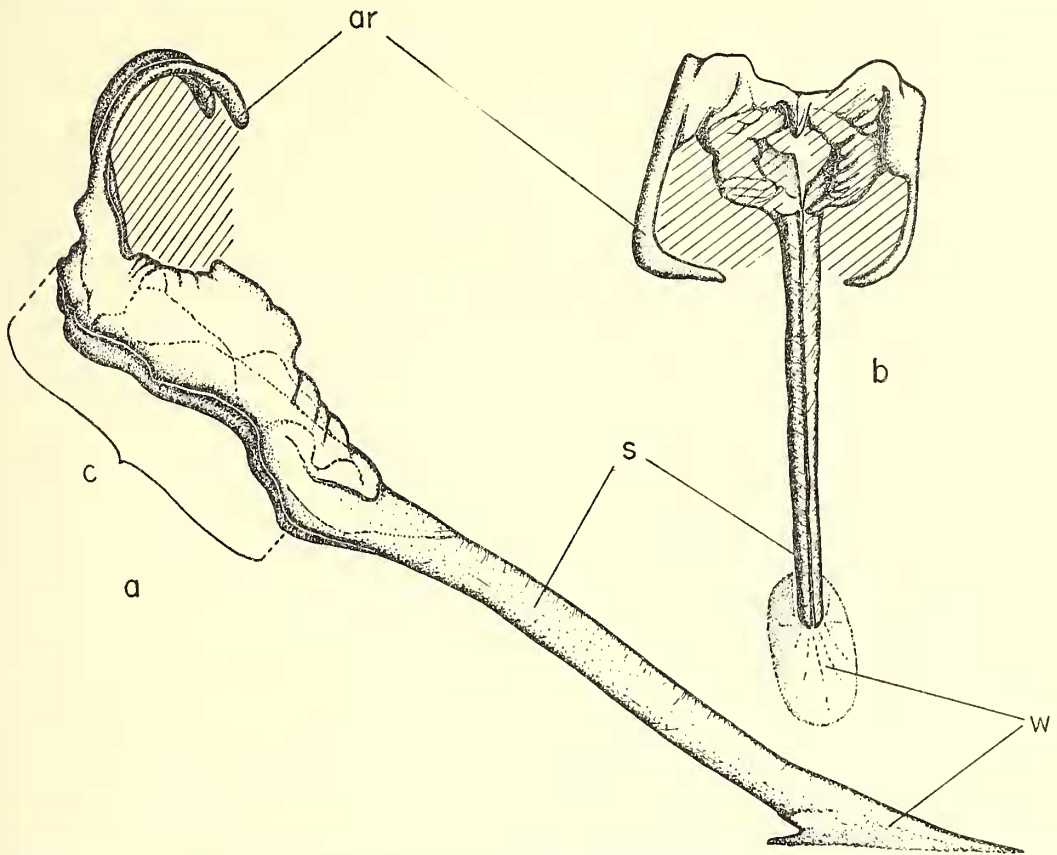
begin his intermittent beating. Such upsets occur more and more infrequently until, eventually, after some hours, she lies passively under all his advances.

*D. variegatus* completed courtship in the laboratory on one occasion only and then a part of the behavior was not seen. Courtship climaxed by mating has, however, been watched in *A. barbadensis* on five occasions. The patterns of courtship and mating were virtually identical—except for points of difference introduced by deliberate interference. It seems likely that the behavior in the two species is the same.

There is no mating grasp at all in these scorpion-spiders and the animals remain un-

connected throughout as in some of the pseudo-scorpions and mites.

Once the female is truly passive, mating can begin. The male lowers his body and touches it to the ground several times. He gets up, moving closer to and almost touching the body of the female who remains motionless. He turns round so that he faces directly away from her and, lowering his body, crouches down on the substratum as before. A slender, transparent spermatophore is then extruded from his genital opening. Once the distal end of the spermatophore is cemented onto the ground, the male scorpion-spider raises himself and turns round so that he again faces the female. He then moves for-



TEXT-FIG. 4. Spermatophore of *A. barbadensis*. **a**—Lateral view; the right-hand side is that from which the female approaches to take up the sperm. **b**—Dorsal, slightly lateral, view showing the face approached by the female. The position of the two sperm masses is indicated by the cross-hatched areas just above the capsule portion of the spermatophore, **c**, where they are normally held by the arms, **ar**, of this region. Stem of spermatophore, **s**; flat basal portion which is cemented down onto the substratum, **w**.

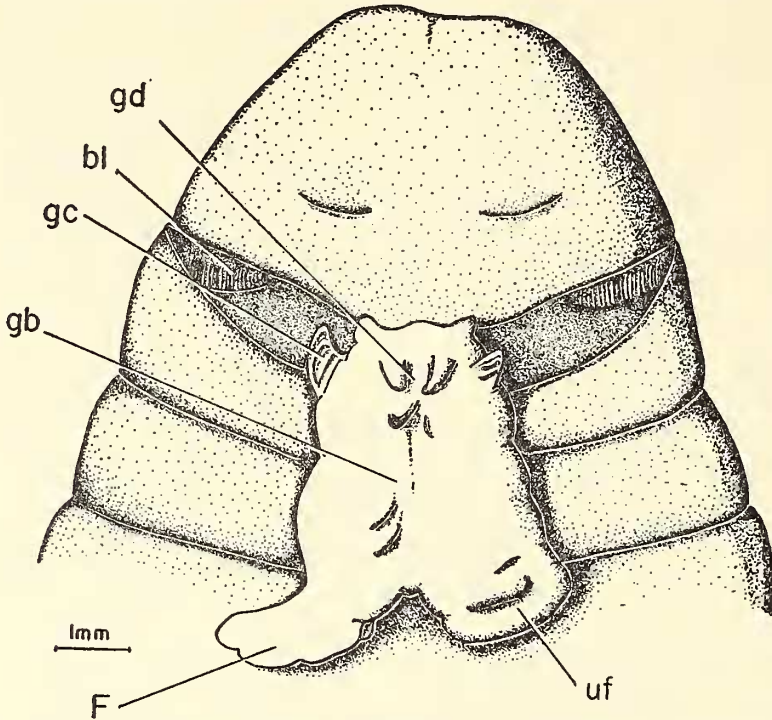
ward and crouches on top of the spermatophore, moving his body slightly as if orienting himself correctly in respect to it. Once settled, the male normally remains motionless for up to five minutes. Apparently it is during this time that he places two masses of sperm in position on the proximal end of the spermatophore. Certainly up to this point the spermatophore has been empty of sperm.

The male slowly rises from the spermatophore and steps back a few centimeters. He quivers and the female which has so far remained immobile comes forward, her feelers guiding her towards the spermatophore (Text-fig. 4). Finally she crouches over it, applying her genital region to its proximal end. She jerks forward against it, usually several times in quick succession though sometimes there is a thirty-second interval between the first and second attempt.

She then stands up with the two masses of sperm caught partly beneath her genital oper-

culum. The male becomes active once more and taps the female rapidly for about fifteen seconds. When she moves away from the empty spermatophore, the male eats it. The two animals then separate and there is no evidence of aggression.

Finally, in this section on the reproduction of the Phrynichida, it may be mentioned that electrical stimulation of the genital area of a living male *D. variegatus* can cause the production and extrusion of a spermatophore. When low intensity shocks are first applied, the operculum will be lifted slightly and the genital cones be extruded. Presently, from between and posterior to these, a larger organ begins to appear. This is a many-lobed structure which will be referred to here as the "genital body" (Text-fig. 5). Further gentle stimulation causes the secretion of an amount of transparent, very sticky material, presumably that which normally cements the spermatophore to the substratum. Then, also from between the lobes of the genital body, the



TEXT-FIG. 5. The genital region of a male *D. variegatus* showing the "genital body", **gb**, which has been extruded from the genital opening after electrical stimulation. The lobes of the genital body are somewhat asymmetrical in this example, so that the flap, **f**, of the right side is still tucked in on the left, **uf**. The genital cones have been displaced laterally and anteriorly and are only just recognizable, **gc**, in the drawing. The spermatophore is extruded at the point marked, **gd**, in the mid-line and between the various lobes. The striations, **bl**, represent part of the first pair of book-lungs which are visible under the genital operculum.

actual spermatophore itself is extruded. In such artificial conditions the production is never successful and the structure could clearly not be used for transference of sperm by the animal concerned. The use of such stimulatory techniques was reported by Piza (1950) working on a scorpion, *Tityus bahiensis*. Here a structure, which subsequent work has identified as the spermatophore, was partly extruded from the animal. In the case of a South African scorpion subjected to similar treatment, not only was the skeleton of the spermatophore ejected, but also a large part of the glandular apparatus which secretes it. Thus it should be borne in mind that the eversion of the "genital body" in *D. variegatus* may well be an artifact due to the abnormal stimulation and that in natural production of a spermatophore this does not occur.

#### DEVELOPMENT

It is known that in the Phrynichida, Schizo-

mida and Thelyphonida, the eggs are attached beneath the abdomen of the female after they are laid, a phenomenon that occurs also in the pseudoscorpions. The eggs of *A. barbadensis* and *D. variegatus* are held together in a fairly tough egg-case consisting partly at least of chitin. According to Millot (1949) and Lawrence (1953) the cavity within the egg-case is continuous with that of the female genital organs until the young are freed. In the case of *A. barbadensis* this is not so; the anterior end of the egg-case is a tough dried stalk which is held in position just beneath the genital operculum by the pair of sclerites mentioned earlier (p. 29 and Text-fig. 3c). This coupling of the anterior end may occasionally come loose and the animal is apparently incapable of hooking it up again. When this happens, the case is merely left attached by sticky threads to the abdomen. Occasionally, however, the whole attachment fails and the egg-case is dropped to the ground. In



one such instance, the female then ate the young and their case.

As Lawrence and Millot have observed, the abdomen of *D. variegatus* may be considerably hollowed out so that the egg-case does not project much below the normal level of the abdomen. The lateral margins tend, in fact, to overlap the edges of the egg-case and thus insure better protection. In *A. barbadensis* this hollowing of the abdomen is far less marked and the egg-case tends to hang down below the normal level of the abdomen, especially just before hatching.

The egg-case is secreted when the eggs are laid. It appears as a semi-transparent, colorless material which toughens and darkens during the subsequent twenty-four hours. It consists of two layers, an outer one which encloses the whole and a thinner inner layer which is continuous with packing material which lies between the eggs and the stalk attaching the case to the female.

It is not known how long the eggs remain within the case but they can certainly be carried for as long as a month before hatching. Emergence from the egg-case takes place during the night or early morning as a rule. The young come out through a ragged slit at the posterior end of the case. About twenty-four hours before the hatching this part of the egg-case can in fact be seen to have become softened and partly freed from the abdomen. Emergence may take as long as the whole night, the young easing slowly out of their own first exuvia as well as the partially liquified case. As they become free, they climb back onto the female. The remnants of the egg-case, the egg-shells and exuvia remain attached to the female until the young desert her several days later.

The young scorpion-spiders, *A. barbadensis* numbering from 15-30, *D. variegatus* up to 50, cling onto the abdomen of the female, covering both the ventral and dorsal surfaces, a phenomenon which occurs also among thelyphonids, as shown by the illustrations given by Strubell (1926) and Yoshikura (1958). They have never been seen on the prosoma and if one is dropped there experimentally, it will immediately climb back to the abdomen. It is not clear why this is so, either in terms of what controls the behavior of the young or what selective advantage is given by such a distribution of the young on the parent. Among scorpions, the female does not appear to be incommoded by the young which cling onto her prosoma any more than by those on the abdomen.

Newly hatched *A. barbadensis* are very soft

and dusky pink; in *D. variegatus* the abdomen is light green. The abdomen is relatively much longer at this stage than it is in the adult and eleven segments are far more easily recognized. The feelers are folded up and, like the pedipalps, they are not used during this instar. The legs, however, attach the young very effectively to the female and one of the young animals can be disengaged only with great difficulty. If indeed a few are detached and strewn around the female, they make but feeble attempts to climb up again and only occasionally succeed. The female does not help in this at all, and in fact she merely shakes them off her legs if she can. She may touch one tentatively with her feeler for several seconds, then suddenly lunge forward, catch it on the spines of the pedipalps and immediately begin to eat it. Observations in which one or more of the young were eaten were made on four females and there is no evidence that they would not have eaten the entire broods if given the chance. In two cases the young had been hatched outside the laboratory so that there is little possibility that the behavior was abnormal. This leads to the conclusion that there is no maternal behavior towards young scorpion-spiders that leave their perches on the back of their mother.

This is in marked contrast to the complex maternal patterns shown by many other arachnids, such as some of the spiders and scorpions. In terms of selective advantage, the explanation for this does not seem to lie in the young scorpion-spiders being more firmly fixed to the parent than are young scorpions; both appear equally well attached. It seems possible, however, that the two different types of response can be correlated with the reactions of the mothers to a threatening danger or a disturbance. In such circumstances, a scorpion will stand and threaten with claws or sting, otherwise it remains immobile. In only a few cases will it run away, and if flight occurs, it is usually brief.<sup>5</sup>

A scorpion-spider, on the other hand, stands and tries to defend itself only if it has already been partly damaged. Very occasionally it will remain still and perhaps be overlooked; almost always, however, it starts to run immediately. The flight is broken up into short dashes sideways but as a rule the animal finally comes to rest several yards from the site of the original

<sup>5</sup> Possible exceptions to this generalization are such flattened, rock-dwelling scorpions as the South African genus *Hadogenes*, which may display an escape response. This, however, is not shown by females carrying their young, so that at such a time their behavior is similar to that of the other scorpions mentioned above and not to be compared with that of the phrynichids.

disturbance. The point is that, if young scorpion-spiders are knocked off their mother, they usually have no chance to climb back because their mother will normally be some distance away by the time they are ready to do so. It is of no advantage for the female to have developed behavior which would allow her to distinguish her own young from any other helpless, wiggling arthropod which might be food on the ground. In the case of the scorpion, mother and young are still together after an "attack" has passed and it would be advantageous for a female to possess a behavior pattern that actually helps the young to remount, and even more so for her to recognize that they should not be eaten. A further consideration which may prove important in such an explanation of why the phrynichid female has evolved no recognition of her young is that these animals, unlike scorpions, possess no "homes" in which they live and to which they return. It would thus be of interest to know of the Thelyphonida and the Schizomida—more especially as females from both these orders are reported to live in burrows, at least when they have eggs (see Gravely, 1915; Millot, 1949; and Yoshikura, 1958).

On their mother's back, the young phrynichids make almost no movement during the second in-termolt period. This lasts four to six days in *A. barbadensis*, up to 12 days in *D. variegatus*. The second molt appears always to begin during the morning. The length of time taken for any one individual molt varies considerably, from six minutes to almost three hours. There seems to be a preferred site for this event—the posterior part of the abdomen of the female—and most of the young do not begin to shed their skins until they can move towards this position. The molt begins with a number of cheliceral movements. Then a blister-like swelling arises on the carapace. This pulsates slightly and a split gradually appears round its anterior margin. The animal bulges out of this slit. Of the limbs the first to be freed are the chelicerae, then the pedipalps and lastly the legs. As the old cuticle is sloughed back, fluid within the body of the young can be seen to be pulsating rhythmically. When the new cuticle is uncovered, it is almost colorless but rapidly becomes greenish-blue and darkens over the next couple of days to a brilliant metallic green. The old skins are not eaten by mother or young and they fall from the mother's back as pieces of pink fluff. Like the first exuviae of scorpions and unlike their own late stages, the skins that are left after this molt are very thin, soft and flexible. This is presumably a reflection of the fact that the animals are markedly unsclerotized during their early instars.

Unlike many scorpions which remain for some time on the female after they molt, the young scorpion-spiders climb off within a few minutes of freeing themselves of their cast skins. This climbing down is no accident and is quite "deliberately" done, for a young third instar nymph will immediately run off its mother if replaced.

There is a marked change in the behavior of the phrynichids after their second molt. Once they reach the ground, they run around quickly, feelers are unfurled and they tap tentatively at objects near them. There is a noticeable avoidance of light. None of this behavior was of course present when the young were on their mother. Within two days they are capable of catching and eating termites provided for them, and are clearly independent of the female and, indeed, can be found at this stage running about by themselves in the field.

#### PHYLOGENETIC DISCUSSION

It has already been said that the study of the behavior of the Pedipalpi might throw light upon the phylogenetic relations of the different groups which have been lumped in this order. Many of the observations here recorded merely serve to emphasise the need for comparable studies on the other two members of the Pedipalpi, the Thelyphonida and the Schizomida. Of the biology that has been described, however, three aspects appear as though they might provide material of significance in relation to the phylogeny of these groups, namely, feeding, sexual behavior and the general reactions of defence and offence. The importance of feeding has already been implied in the stress which Petrunkevitch lays on the feeding organs in his classificatory system. It is, however, abundantly clear that more work is still needed on the mechanism of feeding in the Phrynichida, while even less is known of the details in thelyphonids and schizomids (Snodgrass, 1948). It is perhaps significant that although the filter-plate apparatus in the Phrynichida is superficially like that of scorpions, there are no associated limb movements in the former.

Courtship likewise can be but sketchily compared in the three groupings because actual mating has not yet been seen in the thelyphonids. From descriptions of the preliminary behavior (Fischer, 1911; Gravely, 1915) it seems that the male in this order grasps the female first with his pedipalps and subsequently with his chelicerae, during which the two animals face each other. Schizomids also promenade before mating takes place (Sturm, 1958) and a cheli-

ceral grasp occurs, but here, however, the grasp is quite different from that reported for thelyphonids. It is the female which holds the male and the part which is grasped is the specialized portion of his tail; consequently both animals face in the same direction. Hence it is possibly of little significance that the Phrynichida also differ widely, in having no mating grasp at all. Indeed such variations in detail of courtship may occur even among arachnids which are undoubtedly closely related; for instance among the pseudo scorpions a mating grasp may or may not be present.

Insemination is indirect by way of a spermatophore stuck down onto the substratum. Considered alone, however, the fact is of little significance as this would appear to be the primitive method among the Arachnida (Alexander & Ewer, 1957) if not among terrestrial arthropods generally (Angermann & Schaller, 1956; Gilarov, 1958). If the arachnids were originally aquatic forms in which fertilization was effected by "casual" meeting of sperm and eggs after both had been liberated into the sea, then the first step in the evolution of the spermatophore is perhaps exemplified by the behavior of water mites and some pseudoscorpions in which the male deposits spermatophores apparently haphazardly around him, with or without the presence of a female. With a drier and wider habitat there would be increased danger of desiccation of the sperm and perhaps decreasing chances of a female coming across such casually deposited spermatophores. Thus there would be selection for an association between male and female to be established before deposition of a spermatophore occurs and it is to be expected that such associations may have been independently evolved several times. Nevertheless the phrynichids and schizomids might be regarded as related insofar as the male has his posterior end towards the anterior end of the female while he deposits a spermatophore. Such behavior is in contrast to that of the pseudoscorpions, the mites and especially the scorpions where the spermatophore would not function if the female were forced to approach it from the opposite direction. However, the very specialized mating grasp of the schizomids makes it improbable that the position taken up during spermatophore extrusion bears any direct relationship to that of the phrynichids.

The marked dissociation of the acts of spermatophore deposition and sperm extrusion is unique and it is hard to see any advantage to the species from such behavior. It is, however, clear that the two events are completely independent. Thus on two occasions a male *Admetus* re-

turned, in one case three times, to a spermatophore when he apparently been unable to load it successfully at the first attempt. Another time a female *Admetus* walked away while the male was depositing sperm; the male chased after her, courted her once more to passivity and then returned to his depositing of sperm. This dissociation possibly offers the advantage that should anything cause a faulty deposition of a spermatophore or disrupt the mating, sperm will not have been wasted. A somewhat similar situation occurs in *Tityus trivittatus* in which Bücherl (1956) has described a "reloading" of the spermatophore after the female had removed the first mass of sperm.

Petrunkevitch has postulated a close association between the Phrynichida and the Araneae, and the present observations can be read in support of such an opinion. It has been suggested (Alexander, 1962) that the sexual behavior of spiders may be derived from that of forms in which there was a dissociation of the act of loading a spermatophore from its deposition. This is the condition in the phrynichids. Further, it is easier to envisage the course of the evolution of spider mating were it derived from a pattern in which the members of a pair did not grasp and this again is a phrynichid character.

Finally we will consider what Manton (1958) would term "habits of life." It is this last type of behavior that is hardest to categorize distinctly, the facts are less definite, actions less stereotyped and more difficult to describe. As Manton says: "Habits of life which appear to have been of evolutionary significance vary greatly in their ease of recognition because they may not be exercised all the time." Nevertheless it is from this level of activity that an understanding of the general biology and the direction of morphological and behavioral evolution will emerge.

In considering the life habits of the groups of the Pedipalpi it is desirable to point out that the natural micro-ecological distribution of the animals is not markedly different. What is significant, however, is that the Schizomida and Thelyphonida remain within their burrows or in spaces in the soil while the Phrynichida run freely over it or hide in crevices—the animals may be referred to as being "of fixed abode" and "vagrant," respectively. Defensive behavior can be correlated with this difference. The "fixed abode" groups stay to defend themselves with cheliceral pedipalps or repugnatorial glands when concealment is no longer possible. The Thelyphonida are aggressive in captivity and large specimens may even damage human hands with their pedipalps. This is in complete contrast

to the emphasis among the phrynichids on camouflage or flight; the scorpion-spiders either sit still and are overlooked or get away quickly and unexpectedly with sudden and disconcerting sideways darts—behavior for which their flattened form, short abdomen and the sideways extension of their legs are well adapted.

The absence of attack as a defensive response in phrynichids is also partly reflected in an "inefficient" use of the pedipalps during prey-catching, for the scorpion-spiders frequently fail to hold prey at which they grasp. In natural conditions there must often be unsuccessful attempts or the prey must be weaker, smaller and consequently hunted more frequently. In either case accurate locating and careful stalking is important and for these two phrynichid characteristics are essential, the habit of roaming freely about and the possession of elongated feelers. Together with the latter must be considered the toilet behavior patterns involved in keeping them clean as well as the specialized pedipalpal brushes.

Though it is freely admitted that this is but the beginning of an understanding of phrynichid life habit, the number of anatomical and behavioral characteristics which can be correlated with this habit suggests that it has been of prime importance in controlling the direction of phrynichid evolution. When similar and more complete analyses are available for the Thelyphorida and Schizomida, it may prove possible to comprehend the true inter-relationships of these groups and their relationships with the other Arachnida.

#### SUMMARY

1. The general biology and behavior of two species of phrynichid, *Admetus barbadensis* Pocock and *Damon variegatus* Perty, have been studied. A description is given of their habitat, food and manner of feeding, their drinking and their cleaning patterns.

2. Behavior which does not lead up to courtship but occurs between two members of the same species is described; much of this behavior consists of threatening contests in which the delicate feelers are used as "weapons."

3. The main course of courtship is described. Insemination is achieved by means of a spermatophore which the male deposits on the substratum and from which the female picks up the sperm mass. This method of mating is compared and contrasted with those occurring in the schizomids, scorpions, pseudoscorpions and some of the mites.

4. Events associated with the electrical stimulation of the genital area of a male *D. variegatus*

are described and discussed in relation to the production of a spermatophore.

5. The manner in which the eggs are cared for after they have been laid and the hatching of the young is described, as well as general observations on their behavior in contrast to that of the adult animals. An hypothesis is put forward attempting to explain, in terms of selective advantages, the absence of any maternal reaction from the female phrynichid to one of her young struggling on the ground in front of her.

6. The behavior recorded here is discussed in relation to its bearing on conclusions about the inter-relationships of the Phrynichida, Schizomida and Thelyphorida.

#### REFERENCES

- ALEXANDER, A. J.  
1962. Courtship and mating in amblypygids (Pedipalpi, Arachnida). Proc. Zool. Soc. Lond. (in press).
- ALEXANDER, A. J., & D. W. EWER  
1957. On the origin of mating behavior in spiders. Amer. Nat., 91: 311-317.
- ANGERMAN, H. & F. SCHALLER  
1956. Spermatophorenbau und bildung bei Arthropoden mit indirekter Spermatophorenübertragung. Ber. 100-jaarf. Deutsh. entomol. gesell. Berlin, 228-237.
- BÜCHERL, W.  
1956. Escorpiões e Escorpionismo no Brazil. Mem. Inst. Butantan, 27: 121-155.
- FISCHER, G. E. C.  
1911. The courtship of whip-scorpions. J. Bombay Nat. Hist. Soc., 20: 888-889.
- GILAROV, M. S.  
1958. Evolution of the insemination character in terrestrial arthropods. Zool. Zh., 27: 707-735. (In Russian, with English summary).
- GRAVELY, F. M.  
1915. Notes on the habits of Indian insects, Myriapods and Arachnids. Rec. Ind. Mus., 11: 483-539.
- LAWRENCE, R. F.  
1949. Notes on the whip-scorpions (Pedipalpi) of South Africa. Trans. Roy. Soc. S. Afr., 32: 1-11.  
1953. The biology of the cryptic fauna of forests. Cape Town: Balkema.
- MANTON, S. M.  
1958. Habits of life and evolution of body design in arthropoda. Journ. Linn. Soc. Lond. Zool., 44: 58-72.

## MILLOT, J.

1949. Ordre des Uropyges et Ordre des Amblypyges. In *Traité de Zoologie*. 6. Ed. P. P. Grassé. Paris: Masson et Cie.

## PATTEN, B. M.

1917. Reactions of the whiptail scorpion to light. *J. Exp. Zool.*, 23: 251-275.

## PETRUNKEVITCH, A.

1955. In *Treatise on invertebrate Paleontology*. Part P. Lawrence: Univ. Kansas Press.

## PIZA, S. DE T.

1950. Reproductive organs and reproduction in *Tityus bahiensis* (Scorpiones, Buthidae). *Proc. 8th Int. Congr. Ent.* Stockholm, 1948: 1026-1027.

## SNODGRASS, R. E.

1948. The feeding organs of Arachida, including mites and ticks. *Smithsonian Misc. Coll.*, 110, No. 10, 1-93.

## STRUBELL, A.

1926. *Thelyphonus caudatus* L- eine biologische Skizze. *Verh. Nat. Ver. Bonn*, 82: 301-314.

## STURM, H.

1958. Indirekte Spermatophorenübertragung bei dem Geisselskorpion *Trithyreus sturmi* Kraus (Schizomidae, Pedipalpi). *Naturwissenschaften*, 6: 142-143.

## YOSHIKURA, M.

1958. Observations on the breeding habits of a whip scorpion *Typopeltis stimpsonii* Wood. *Acta Arachnol.* 16: 1-7.